The genus *Scaphella* (Gastropoda: Volutidae) in the Neogene of Europe and its paleobiogeographical implications

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ABSTRACT

The genus *Scaphella* supposedly has a long geological history on both sides of the Atlantic, extending back to the Paleocene. However, there are differences in both shell morphology and ecological preferences between the New and Old World representatives. This paper traces the history of *Scaphella* in the Atlantic. It is suggested that the group originated in the Cretaceous/Paleocene Tethys Sea, a genus such as *Caricella* dispersing during this time to the New World, and thence giving rise in the Neogene to *Scaphella*. In the Old World the record of *Scaphella* is uninterrupted from the Paleocene to the middle Pliocene, after which the genus disappeared from the Eastern Atlantic. The genus *Scaphella* is heterogeneous, the European species differing in certain constant shell characteristics from the New World species. *Scaphella carlae* new species is described from the lower-middle Pliocene Mediterranean of the Estepona Basin (Spain) and a possible second new species is discussed, but not named due to the poor material available, from the lower Pliocene Atlantic of the Guadalquivir Basin (Spain).

INTRODUCTION

The subfamily Scaphellinae H. and A. Adams, 1858, comprises three extant genera; *Ampulla* Röding, 1798, *Scaphella* Swainson, 1832, and *Volutifusus* Conrad, 1863 (Darragh, 1988). In the Recent fauna they occur in the western Atlantic Ocean, including the southeastern United States, Gulf of Mexico and Caribbean (*Scaphella*, *Volutifusus*), and the eastern Atlantic, from southern Portugal and Spain to the West African coasts of southern Morocco and the Canaries (*Ampulla*). In the early fossil record another genus, *Caricella* Conrad, 1835, predominates, being present from the Cretaceous in the Tethyan record (Bandel, 2003) and in the New World Paleocene to Oligocene (Dockery, 1977). Bandel (2003), however, placed *Caricella* in a separate subfamily, *Caricellinae* Dall, 1907. In this paper we deal with the Old and New World taxa traditionally placed in the genus *Scaphella*.

The gastropods of the genus *Scaphella* today live in warm water, with a Recent subtropical to tropical distribution restricted to the western Atlantic, from the coasts of North Carolina (USA), southward through the Gulf of Mexico to Yucatan (Weaver and du Pont, 1970), the Caribbean, up to Colombia (Clench, 1946; Poppe and Goto, 1992). The genus has an widespread geological record in the Americas, with a few records in the Paleocene, an extensive Neogene history, but is not recorded from the Eocene or Oligocene.

In the Old World the Scaphellinae have an equally long geological record extending back to the Paleocene of the North Sea Basin (Ravn, 1933). The group flourished in the Miocene, extending its distribution into the Atlantic and reaching the southern Atlantic coast of Iberia in the late Miocene (Pereira da Costa, 1866). In the Pliocene the Scaphellinae were abundant in the North Sea Basin (Marquet, 1997). Their range extended into the Atlantic, as far as central western Iberia (Mondego Basin) (Silva, 2001) and into the Mediterranean, where they were restricted to the Alboran Sea (Estepona Basin), except for a single unconfirmed report from Algeria (Lamothe and Dautzenberg, 1907).

The last European records for *Scaphella* are from the upper Pliocene of the North Sea Basin. Today the Scaphellinae are represented in the European faunas by the monotypic genus *Ampulla* Röding, 1791. *Ampulla priamus* (Gmelin, 1791) occurs from the southern coast of Portugal (Nobre, 1938–40), or possibly from the southwestern coast of Portugal, were it is rare (G. Calado, pers. comm., 2006), south to the Canaries and southern Morocco (Poppe and Goto, 1992).

Pliocene Atlantic and Mediterranean records of *Scaphella* are scarce. Chavan and Coatman (1943) and Brébion (1964) recorded *S. lamberti* from the Pliocene of the Loire Basin. Silva (2001) listed *S. lamberti* from the Atlantic Pliocene of the Mondego Basin and Zbyszewski (1943, 1959) from the Lower Tagus-Sado Basin of central-western Portugal. There is only one unconfirmed report by Lamothe and Dautzenberg (1907) of *S. lamberti* in the Mediterranean from the Pliocene of Algeria.

Recent work on the rich lower Pliocene deposits of the

Atlantic Guadalquivir Basin and Mediterranean Estepona Basin (southern Spain) revealed the presence of *Scaphella* in both these basins.

FOSSIL-BEARING LOCALITIES

The material discussed herein originates from three distinct Iberian localities, situated, from northwest to southeast, at:

1. Vale de Freixo, Pombal region, central-western Portugal. Atlantic. Mondego Basin. The Pliocene Carnide Sandstone Formation generally consists of fine micaceous sand without macro somatofossils (body fossils). Locally, the lowermost section of this formation contains a thin fossiliferous sequence consisting of a basal conglomerate and sand rich in fossil shallow marine molluscan shells. At Vale de Freixo, the basal fossiliferous beds of the Carnide Sandstone have a maximum thickness of approximately 1 m. These are dated as lower to middle Pliocene, uppermost Zanclean to lowermost Piacenzian (Silva et al., 2000; Silva, 2001; Silva et al., 2006).

2. Lucena, Huelva region, southern Spain. Atlantic. Guadalquivir Basin. The sandy, near-shore deposits of Lucena are part of the Arenas de Huelva Formation and dated as lower Pliocene, Zanclean (Civis et al., 1987).

3. Velerín, Estepona region, southern Spain. Mediterranean. Estepona Basin. These deposits consist of a variety of different lithologies, from fine clayey sands (Velerín carretera outcrop), deposited at relatively greater depths, to coarse conglomerates (Velerín conglomerates outcrop). These conglomerates, which must have been deposited relatively rapidly or in storm conditions (Sanz de Galdeano and Lopez Garrido, 1991), contain the richest fauna, a curious mixture of large and small abraded and perfectly preserved shells. These deposits are dated as middle Pliocene, lower Piacenzian (Guerra-Merchán et al., 2002).

For detailed location maps and a geological and stratigraphical overview of the fossiliferous deposits covered in this paper see La Perna et al. (2003) and Dell'Angelo and Silva (2003), for the Mondego Basin, Civis et al. (1987) for the Guadalquivir Basin, and Sanz de Galdeano and Lopez Garrido (1991) and Guerra-Merchán et al. (2002), for the Estepona Basin.

The Pliocene malacofauna from all three of these basins, according to Silva (2001), La Perna et al. (2003), and Landau et al. (2003), corresponds to the Mediterranean Pliocene Molluscan Unit 1 (MPMU1) of Monegatti and Raffi (2001).

The material herein discussed is housed in the following collections: IRScNB: Institut royal des Sciences naturelles de Belgique; BLP coll.: B. Landau collection; CMS coll.: Carlos Marques da Silva collection, Departamento de Geologia da Faculdade de Ciências de Lisboa; RM coll.: collection R. Marquet (will be incorporated into the collection Institut royal des Sciences naturelles de Belgique in the near future); CG coll. = Chris Garvie collection, USA; M-V coll.: Manuel Molin/Daniela Velo collection, Bonares, Spain; AC coll.: Alain Cluzaud collection, France.

SYSTEMATIC PALEONTOLOGY

The genus *Scaphella*

The type species of the genus *Scaphella* is *Voluta junonia* Shaw, 1808, by subsequent designation of Gray, 1847 (Clench, 1946). *Scaphella junonia* is a western Atlantic species, characterized by axially ribbed post-nuclear whorls, prominent columellar plications and a well developed siphonal fasciole.

Clench (1946) recognized *Scaphella* sensu stricto characterized by shells that were a little more massive, nuclear whorls extended and the calcarella usually worn away; and *Scaphella (Aurinia)* H. and A. Adams, 1853, in which the shell is strong, but not massive, and the nuclear whorls have a strongly developed calcarella. In a more recent work (Weaver and du Pont, 1970), this division into subgenera was confirmed by differences in the radular structure. According to Clench (1946), the typical subgenus has wishbone shaped rachidian teeth, with the central denticle rather long and narrow, and the lateral shanks extending behind rather than to the sides, but no lateral denticles. In the subgenus *Aurinia* the rachidian teeth have a very strong central denticle, with shanks above extending at almost right angles, and at the base two very small lateral teeth, fused to the central denticle (Clench, 1946).

Later, Weaver and du Pont (1970) recognized three subgenera. The subgenus *Scaphella* sensu stricto was characterized by a papilliform protoconch, usually with a spur-like calcarella present, the teleoconch ". . . is sculptured with spiral[sic] lirae and incised lines . . . ", the columella has three or more anterior plaits, and a siphonal notch and fasciole are present (Weaver and du Pont, 1970: 140). The subgenus *Aurinia* differs in having a larger protoconch, with a projecting calcarella, in lacking a siphonal notch and fasciole, and in having no columellar plaits or only weak ones. They recognized a third subgenus, *Clenchina* Pilsbry and Olsson, 1953, which differs from the nominal subgenus by smaller size, less solid shell, usually with an attenuated spire. These shell differences are small, and both Pilsbry and Olsson (1953) and Weaver and du Pont (1970) separated the subgenera mainly by radular morphology. The nominal subgenus is characterized by uniserial Y-shaped radular teeth, without side cusps, *Clenchina* has small Y-shaped teeth with minute side cusps, and *Aurinia* has tricuspid rachidian teeth, with the central cusp broadest and the lateral cusps strong and sickle-shaped (Weaver and Du Pont, 1970).

Poppe and Goto (1992) placed 'shell similarity' above radular structure. They stressed that these subgenera were based mainly on radular characters, with conchologically similar species having quite different radular structure (Bayer, 1971), and recognized only a single genus *Scaphella*, without subgenera.

In the Recent fauna the representatives of the genus *Scaphella* are restricted to the western Atlantic. The number of species recognized varies considerably, from four (Weaver and du Pont, 1970) to 11 (Poppe and Goto, 1992) or 12 (Clench, 1946). All the Recent species, except *S. gouldiana* (Dall, 1887), have a color pattern of squarish red or black spots in spiral rows on a paler background, which has spiral bands in some species, and most species have axial sculpture on the early teleoconch whorls.

Scaphella in the fossil record

New World

Scaphella is well represented in the Neogene Caribbean fossil record. It is found in the upper Miocene Gurabo Formation of the Dominican Republic (Vokes, 1998) and represented by possibly numerous species in the Floridian Plio-Pleistocene (Petuch, 1994). It has not been recorded from the Tropical American Pacific. The earliest representative of the Neogene group of *Scaphella* in the American fossil record is the upper Miocene Dominican Republic species *S. striata* (Gabb, 1873), which is most similar to *S. gouldiana* in having strong axial nodes at the shoulder. Vokes (1998) noted that the shells of *S. striata* do not show the characteristic color pattern and were probably monochrome. All the specimens from the Florida Plio-Pleistocene illustrated by Petuch (1994) have axial sculpture on the early teleoconch whorls and a spotted color pattern.

The history of the genus in the New World before the Neogene is far more complex. Dall (1907) suggested that the Neogene group of *Scaphella* evolved in the western Atlantic from the genus *Caricella* Conrad, 1835, which is widespread in the Eocene and Oligocene western Atlantic assemblages (Gardner, 1937).

Caricella shares a similar shell shape and color pattern of squarish red dots (Dockery, 1977; MacNeil and Dockery, 1984). It therefore seems that this color pattern is a conservative character of the *Caricella-Scaphella* line of volutes (MacNeil and Dockery, 1984). Gardner (1937) described *Caricella (Atraktus) pycnopecta* Gardner, 1937 from the Shoal River Formation of northern Florida and extended the upper range of *Caricella* into the lower Miocene. In our opinion this new taxon may have been based on a juvenile specimen of *Scaphella*. The holotype is 27.0 mm in height. The juvenile specimen of *Scaphella* sp. from the Floridian Pliocene herein figured (Figures 2–3) shows the same reticulate sculpture, which later disappears in the adult stage. Unfortunately we have not examined or been able to trace any larger *Scaphella* specimen from the Miocene of Florida, where they seem to be very rare.

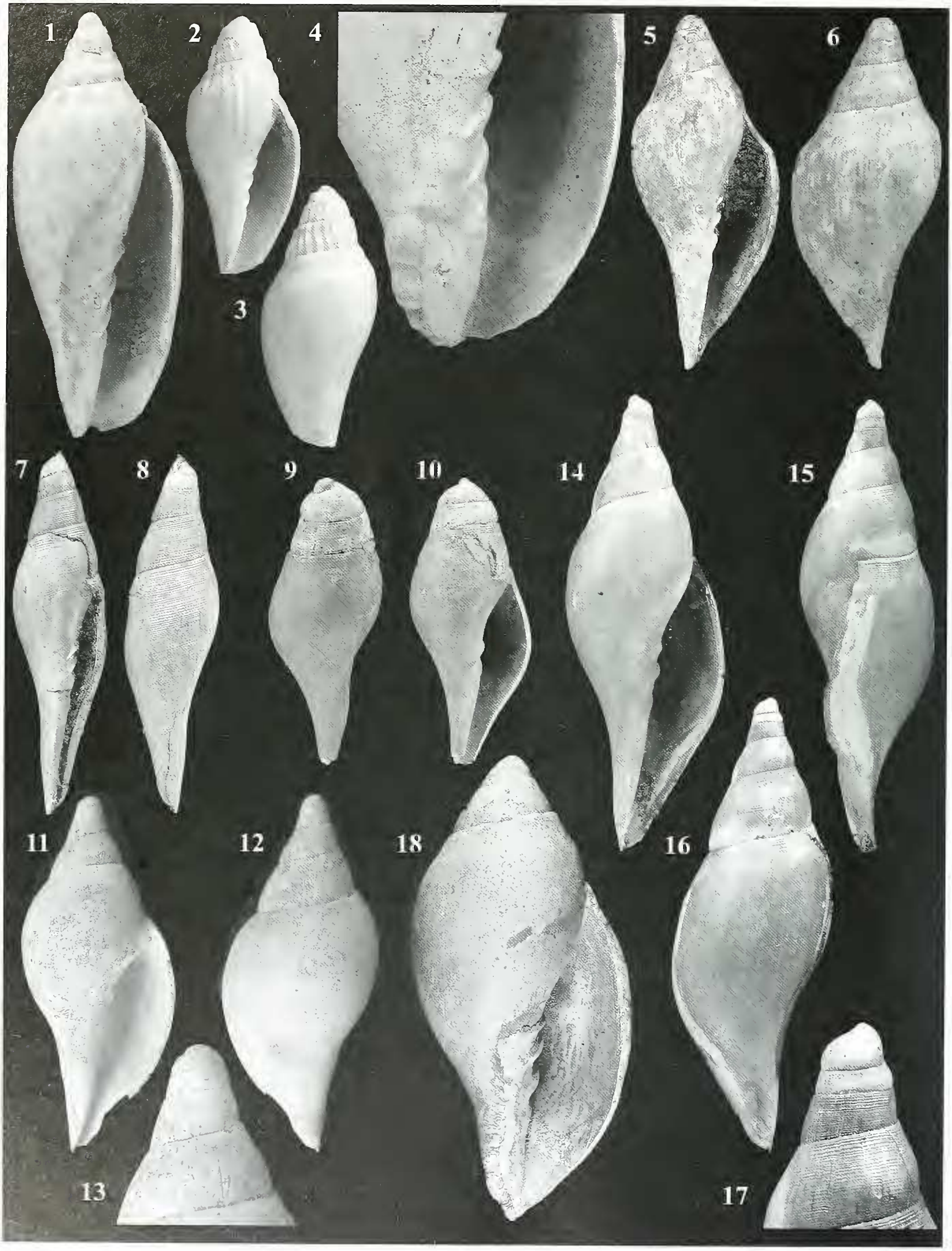
Two species present in the Paleocene of the eastern United States (Porters Creek Formation, Matthews Landing Marl Member, Alabama) are much more similar in their tall, elongated shape to the *Scaphella* representatives in the Old World. We refer to the former two species as the Paleocene New World *Scaphella* group. The shell of *Scaphella showalteri* (Aldrich, 1886) (Figures 5–6) is very similar to the shells of the European species, but does have faint axial sculpture on the early teleoconch whorls, whereas the specimens of *Caricella leana* Dall, 1890, (Figures 7–8) are very elongate, similar to the shell of North Sea Basin Miocene *Scaphella* specimens and most unlike any of the American Eocene-Oligocene *Caricella* species.

Old World

Traditionally, all the European *Scaphella* species had been assigned to the genus *Scaphella* sensu stricto Swainson, 1832. Darragh (1988) placed the European species in the subgenus *Aurinia* H. and A. Adams, 1853. However, as already noted by Darragh (1988) and Marquet (1997), this allocation is problematic. There are certain shell features the Old World *Scaphella* species share that are absent in the New World Neogene species. This will be fully discussed further on.

The earliest records of the genus *Scaphella* in Europe are *Scaphella crenistria* (Von Koenen, 1885) and *Scaphella faxensis* (Ravn, 1902) from the Paleocene of Denmark (Ravn, 1933). The shells of these Paleocene species have the typical fusiform shape, but only three columellar folds (Ravn, 1933) rather than the four or five ones present in the shells of Neogene and Recent species. *Scaphella wetherellii* Sowerby, 1836, from the lower Eocene London Clay shows the typical *Scaphella* shape and also has three columellar folds (Edwards, 1855, pl. 23, fig. 4.). *Scaphella honi* Glibert, 1938 from the upper Eocene, Bartonian (Wemmelian) of Belgium is somewhat unusual, with a carina on the last whorl bearing large sub-obsolete tubercles (Glibert, 1938, pl. 4, fig. 2), but the protoconch and early teleoconch whorls are similar to those of other European specimens, and like the other early *Scaphella*, it has only three columellar folds. *Scaphella* is then represented in the North Sea Basin continuously from the Lower Oligocene, Lattorfian, of Germany, by *S. siemssenii* (Boll, 1851), which has an elongate shell with a tall spire, no axial sculpture at all, and no siphonal fasciole (Beets, 1950), to the Kruisschans Sands (Marquet, 1997), Piacenzian, middle Pliocene (Van Vliet-Lanoë et al., 2002). In the late Oligocene *Scaphella* reached the Atlantic, where it was represented by an undescribed species (Figures 11–13) from the upper Oligocene, Chattian of St-Paul-lès-Dax, Aquitaine Basin, France (AC coll.).

In the Miocene *Scaphella* is represented in the North Sea Basin by *Scaphella bolli* (Koch, 1861) (Figures 14–17), and in the Atlantic by *S. miocaenica* (Fischer and Tournouër, 1879) in the middle Miocene, Serravalian, of the Loire Basin and *S. tarbelliana* (Grateloup, 1840) in the lower Miocene, Burdigalian of the Aquitaine Basin (Peyrot, 1928). The southernmost Miocene record is that of *Voluta lamberti* Sowerby, 1816 in the upper Miocene, Tortonian, of southern Portugal, Algarve Basin (Pereira da Costa, 1866).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In the Pliocene, *Scaphella lamberti* (Sowerby, 1816) (Figures 19–22) flourished in the North Sea Basin and was abundant in the Oorderen Sands of Belgium (Marquet, 1997). In the Atlantic it is recorded from the Loire Basin, northwestern France (Chavan and Coatman, 1943). *Scaphella* is also recorded from central-western Portugal, Mondego Basin (Silva, 2001) and lower Tagus-Sado Basin (Zbyszewski, 1943, 1959), southern Atlantic coast of Spain, Guadalquivir Basin (BLP coll.) and the Alboran Sea, Estepona Basin (BLP coll.). Lamothe and Dautzenberg (1907) recorded *S. lamberti* from the Pliocene of Algeria, although we have not found any further record to confirm this.

The origin of *Scaphella*

The subgeneric assignment of the European fossil *Scaphella* species is problematic. Darragh (1988) placed the European Cenozoic *Scaphella* species in the subgenus *Aurinia*, which according to him is characterized by the absence or reduction of the columellar plicae and the absence of a siphonal fasciole.

Marquet (1997) already noted that Pliocene North Sea Basin specimens of *Scaphella lamberti* do not fit neatly within these characters, having strongly developed columellar plications. The same can be said for the rest of the European *Scaphella* species, which all have strongly developed columellar plications.

One species, *Scaphella (Aurinia) johannae* Darragh, 1988, occurs in the Australian Aldingan, upper Eocene. It is similar in shape to the European species and has no sculpture on the early teleoconch whorls. As noted by Darragh (1988, p. 217), that species is more akin to the European stock of *Scaphella* than to the New World *Scaphella* species, and could be regarded as an example of a Tethyan element in the Australian Eocene fauna.

Thus, the shell characters of the Old World fossil species of *Scaphella* do not fit into any of the three existing subgenera of the genus. The early teleoconch whorls have no axial sculpture; the aperture combines strong columellar folds with the absence of a fasciole, and no color pattern whatsoever has been observed in any specimen under either normal or UV light.

Bondarev (1997) discussed the biogeography and history of the subfamily Scaphellinae, stating that they originated in the Tethys, and placed their roots in the Mesozoic. Bandel (2003) supported the Mesozoic Tethyan origin of the Volutidae with the description of a Cretaceous volutid assemblage from Egypt, from the southern shelf area of the Tethys Ocean, on the African continent. He also described the first and oldest member of the genus *Caricella* from this upper Cretaceous Tethyan assemblage; *Caricella (Misrimelo) klitzschi* Bandel, 2003.

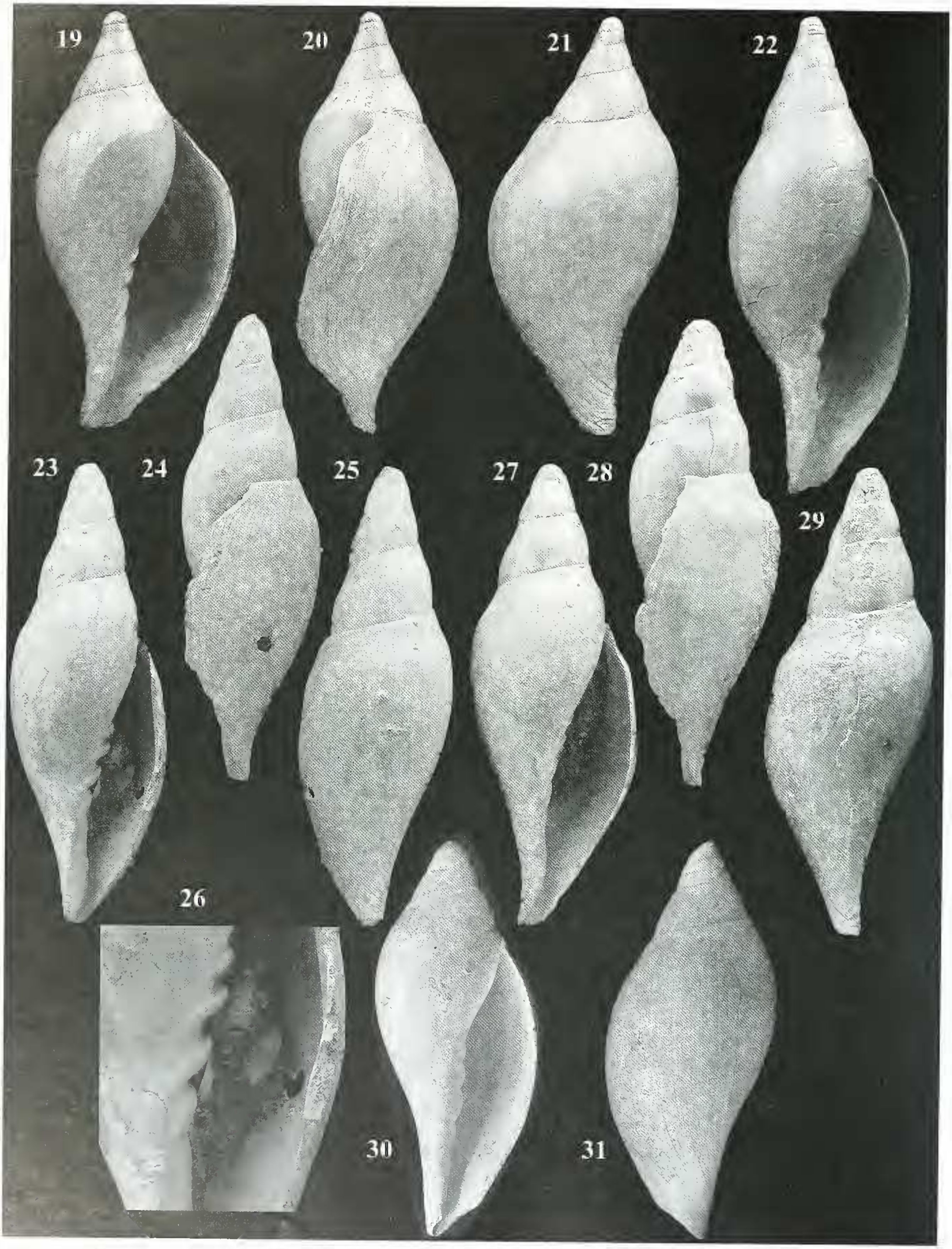
The origin of *Scaphella* is therefore even less clear. Any hypothesis on dispersal of the Scaphellinae must encompass: the first appearance of *Caricella* in the Tethyan Realm; the presence of *Caricella* and *Scaphella* in the New World Paleocene, *Caricella* only in the New World Eocene to Oligocene, *Scaphella* only in the New World Miocene to Recent; the continuous presence of *Scaphella* in the Old World from the Paleocene to Pliocene, but not of *Caricella*.

It is plausible to assume, as suggested by Dall (1907), that the Neogene New World *Scaphella* group evolved from a *Caricella*-like ancestor, which migrated westward from the Cretaceous Tethys into the proto-Caribbean Sea along the predominantly westward flow of ocean currents, long before the closure of the Central American Seaway, when a more-or-less continuous tropical sea existed at low latitudes (Vermeij and Rosenberg, 1993).

Based on the new data of Bandel (2003), it is however more likely that both *Caricella* and *Scaphella* originated in the Tethys Sea, and that both independently dispersed to the New World, which could explain their presence there in the Paleocene, and the similarity between the Paleocene New and Old World *Scaphella* species. Subsequently, as there is no record of any *Scaphella* in the New World in the Eocene and Oligocene, the Neogene New World *Scaphella* evolved from the New World *Caricella*, explaining the differences between this stock of *Scaphella* species and the European stock, which remained more closely similar to the original Tethyan *Scaphella*.

However, none of the Recent Volutidae produce planktonic larvae that could favor this westward transatlantic dispersal (Bouchet and Poppe, 1988; Darragh and Ponder, 1998). Some Cenozoic *Athleta* species produced planktonic larvae (Hansen, 1978); possibly some *Lyria* species (Bouchet and Poppe, 1988); some *Calliotectum* species (Bouchet and Poppe, 1995); and *Provocator*, which appeared in New Zealand late in Pliocene time (Maxwell, 2003). However, we must note that the Ath-

Figures 1–18. *Scaphella* species. **1.** *Scaphella (Scaphella) junonia* (Shaw, 1808) (BLP coll.). North New River Canal, South Bay, Palm Beach County, Florida, USA, Bermont Formation, Pleistocene, height 79.6 mm. **2–3.** *Scaphella* sp., juvenile (BLP coll.). APAC Pit, Sarasota, Sarasota County, Florida, USA, lower Pliocene, Pinecrest Beds, height 32.1 mm. **4.** *Scaphella (Scaphella) martinshugari* Petuch, 1994 (BLP coll.). Early Pliocene, Pinecrest Beds Unit 10, Quality Aggregates Phase 6, Sarasota, Sarasota County, Florida. Detail to show ratchet-shaped columellar folds. **5–6.** *Scaphella showalteri* (Aldrich, 1886), (CG coll.). Dixon's Creek, Alabama River, Wilcox County, Alabama , Porters Creek Formation, Matthews Landing Marl Member, Paleocene, height 22.8 mm. **7–8.** *Scaphella leana* (Dall, 1890), (CG coll.). Dixon's Creek, Alabama River, Wilcox County, Alabama, Porters Creek Formation, Matthews Landing Marl Member, Paleocene, height 26.9 mm. **9–10.** *Scaphella siemssenii* (Boll, 1851), juvenile (BLP coll.). Krefeld, Germany, Chattian, upper Oligocene, height 19.3 mm. **11–13.** *Scaphella* sp. (AC coll.), Estoti, St.-Paul-lès-Dax, Landes, Chattian, upper Oligocene, height 67.0 mm (photo A. Cluzaud). **14–17.** *Scaphella bolli* (Koch, 1862), (BLP coll.). Borgerhout Ring Highway, Antwerp, Belgium, Beechem Formation, Antwerp Sands, middle Miocene, height 80.4 mm. **18.** *Scaphella miocaenica* (Fischer and Tournouër, 1879) (RM coll.). Mathelin, Loire Basin, France, Serravallian, middle Miocene. Height 102 mm (photo Robert Marquet).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letidae were considered as an independent family from the Volutidae by Riedel (2000) (but as a subfamily of the Volutidae by Bouchet and Rocroi [2005]).

In fact Bondarev (1997) stated that volutids are characterized by their high level of provincialism. Bouchet and Poppe (1988, p. 30) pointed out that "Volutes are the most holobenthic of all gastropods . . .", and Darragh (1988) noted that the volute fauna of the areas where species occur today was largely established by mid-Tertiary time, little having been added since. The fact that, as far as we know, *Scaphella* in the New World never dispersed into the Pacific during the Neogene, and in the Old World it did not disperse into the Mediterranean (except the Alboran Sea) or Paratethys, is a testament to its poor dispersal ability. This has not, however, prevented the dispersal of some volutids over long distances, such as representatives of *Alcithoe* and *Lyria*, that probably "hopped" along underwater bridges or chains; these may have a short-lived demersal free-swimming larval stage (Bouchet and Poppe, 1988).

Bandel (2003) suggested that the protoconch-type of the Cretaceous Egyptian Volutidae (including a *Caricella*-like species) suggested a non-planktotrophic development and that they spread only by crawling young and not by free-swimming larvae.

If Bondarev (1997) and Bandel (2003) are correct in their hypothesis that the Scaphellinae originated in the Cretaceous of Tethys Sea, and Dall (1907) is correct in his hypothesis that *Scaphella* originated from *Caricella*, it is likely that the New World Paleocene *Scaphella showalteri* evolved from a Cretaceous/Paleocene Old World ancestor, which emigrated to the New World from the Tethys and in turn gave rise to the New World *Scaphella* stock. The European species traditionally assigned to *Scaphella*, showing consistently distinct conchological characteristics, therefore would constitute a separate stock from those in the New World fauna, and might even warrant a distinct genus-level taxon.

Family Volutidae Rafinesque, 1815
Subfamily Scaphellinae Gray, 1857
Genus *Scaphella* Swainson, 1832

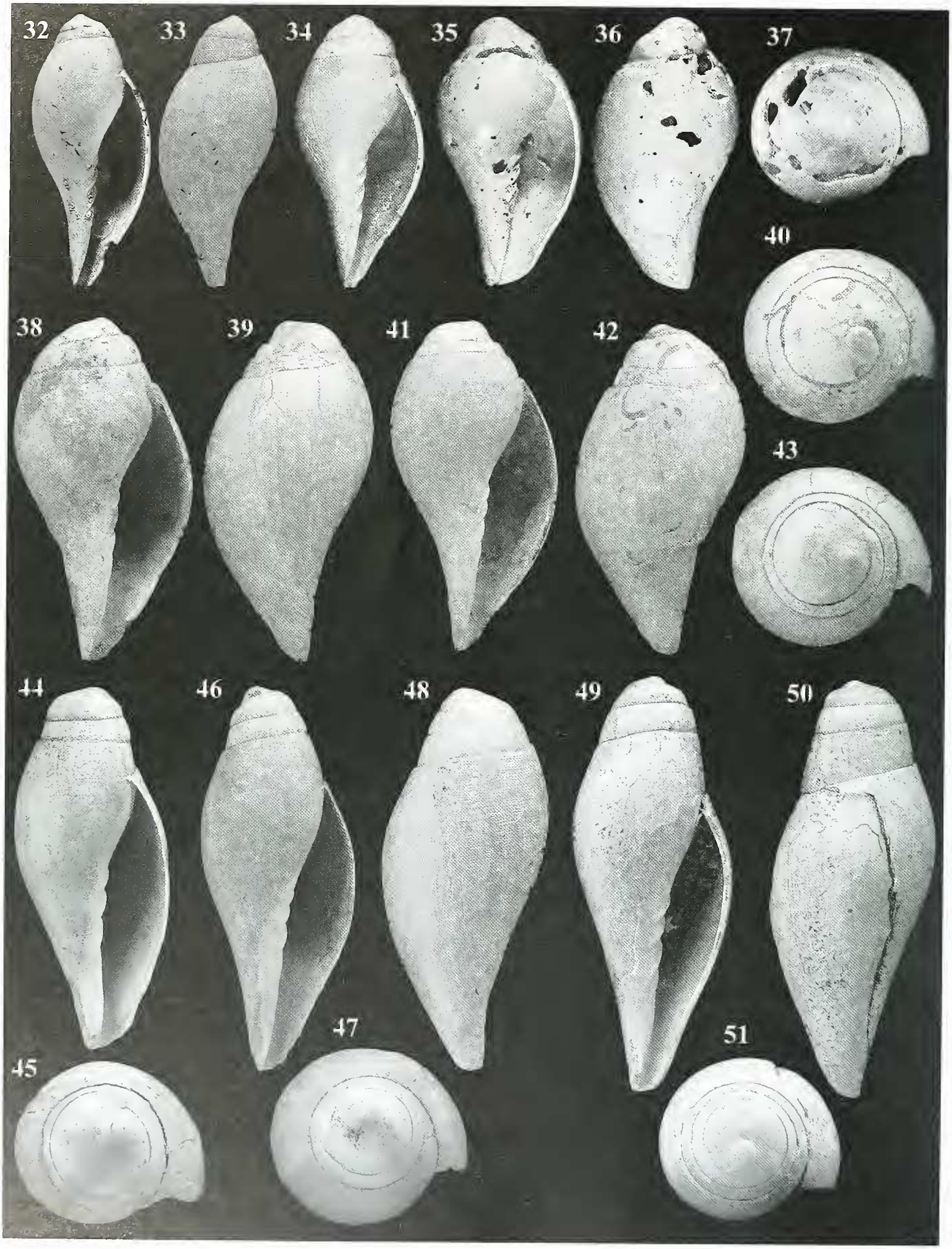
Type species: *Voluta junonia* Shaw, 1808, by subsequent designation, Gray, 1847 (Clench, 1946). Recent, western Atlantic Ocean.

Discussion: Whilst including the European species traditionally assigned to *Scaphella* within this genus, we stress that they differ from *Scaphella* sensu stricto and the subgenus *Clenchina* in not having axial sculpture on the early teleoconch whorls, and in having no siphonal fasciole and no color pattern, and from the subgenus *Aurinia* by again not having axial sculpture or color pattern and having well developed columellar folds. Although the number of columellar folds is similar in *Scaphella* and its subgenera to that in the European Cenozoic species, and in both the folds become more oblique abapically, there is a subtle difference in their shape. The folds in New World *Scaphella* specimens are highly asymmetrical; the anterior face is much less steep than the posterior face, giving the folds a ratcheted appearance (Figure 4). This is not true in the European shells, in which the folds are elevated and symmetrically rounded. This ratchet-like character of the columellar folds of the New World *Scaphella* shells is not present in *Caricella*, in which the folds are symmetrical and much finer than in *Scaphella*.

Although the absence of color pattern in fossil shells is not always a reliable guide to the color of the living animals, almost all fossil *Scaphella* species from the New World (except *S. striata*) are characterized by shells with persistent color pattern (see Olsson and Petit, 1964; Campbell, 1993; Petuch, 1994). Many other shells from the Estepona and Mondego deposits have the color pattern preserved and one would have expected some of the strong spotted pattern of *Scaphella* to be seen if present, but none has been observed in the specimens from Estepona, Mondego, or in any other European fossil *Scaphella* species.

Unlike Recent American *Scaphella* species, which are tropical to subtropical, European fossil *Scaphella* species were predominantly warm-temperate to subtropical. Two of the three more southern deposits where European *Scaphella* have been found (Mondego and Estepona Basins), which were subtropical and tropical respectively (see Silva and Landau, In press), reflect areas where there was some degree of upwelling of cooler nutrient-rich waters (Landau et. al, 2004; Silva et al., 2006). This ability of gastropods of temperate waters to survive in a tropical zone subjected to the periodical upwelling of colder nutrient rich waters has already been observed for species of the genus *Amalda* (Landau and Silva, 2006). Even though European *Scaphella* were widespread and diverse during the early Pliocene, the genus did not survive subsequent Plio-Pleistocene cooling, and the youngest record is of *S. lamberti* from the upper Pliocene Kruisschans Sands of Belgium, where it is rare (Marquet, 1997). Interestingly, European *Scaphella* did not follow the prevalent trend of southward migration seen in many other gastropod taxa as a

Figures 19–31. *Scaphella* species. **19–21.** *Scaphella lamberti* (Sowerby, 1816), (BLP coll.). 'Broad form', Vrasenedok, Kallo, Oost-Vlaanderen, Antwerp, Belgium, Oorderen Sands, middle Pliocene, height 133.0 mm. **22.** *Scaphella lamberti* (Sowerby, 1816), (BLP coll.). 'Narrow form', Vrasenedok, Kallo, Oost-Vlaanderen, Antwerp, Belgium, Oorderen Sands, middle Pliocene, height 176.0 mm. **23–26.** *Scaphella carlae* new species, holotype, IRScNB IST 6994, Velerín Conglomerates, Velerín, Estepona, Spain, lower Piacenzian, middle Pliocene, height 147.0 mm. **26.** Detail showing rounded columellar folds. **27–29.** *Scaphella carlae* new species. Paratype (BLP coll.), Velerín Conglomerates, Velerín, Estepona, Spain, lower Piacenzian, middle Pliocene. Height 138.0 mm. **30–31.** *Scaphella tarbelliana* (Grateloup, 1840) (AC coll.). Moulin Debat, Salles, Serravallian, middle Miocene, height 85.0 mm (photo A. Cluzaud).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result of the late Neogene cooling events (Monegatti and Raffi, 2001; Silva and Landau, in press), and does not survive off West Africa.

Scaphella carlae new species
(Figures 23–29, 49–51)

Description: Shell large, fusiform, of medium thickness, slender and elongate. Protoconch with 1.5 smooth flattened whorls. Nucleus of medium size, with a small, blunt-pointed calcarella. Junction with teleoconch not sharply delimited. Teleoconch with five whorls. The first teleoconch whorl is short and flat, about three times wider than tall. Second teleoconch whorl increases in height rapidly, so that suture, nearly horizontal on first whorl, becomes more oblique. By third teleoconch whorl, width is 1.5 times height. Abapically the whorls become taller and more convex, with narrow, slightly concave sutural ramp. Last whorl about 77% of total height, elongate, slender and not particularly inflated, slightly shouldered in some specimens. Sculpture of very faint to obsolete spiral threads, most evident on early whorls and below suture. Aperture 66% of total height, tall, relatively narrow. Outer lip not thickened, convex in profile. Columella weakly concave, bearing 4–5 oblique, symmetrical, elevated columellar folds of variable thickness, increasingly oblique abapically; middle folds most strongly developed, abapical fold absent in smaller specimens; folds strongest and somewhat flattened in gerontic specimens. Columellar and parietal callus very thin and worn in most specimens. Siphonal canal long and slightly recurved abapically. Siphonal fasciole absent.

Type Material: Holotype; IRScNB IST 6994, height, 147.0 mm; paratype; IRScNB IST 6995, height, 147.0 mm.

Type Locality: Velerín conglomerates, Velerín, Estepona, province of Málaga, Spain.

Stratum Typicum: Velerín Conglomerates, lower Piacenzian, lower Pliocene.

Other Material Examined: Thirteen specimens, from the type locality, BLP coll.

Distribution: Lower Pliocene: western Mediterranean, Estepona.

Etymology: Named after Carla Santos, botanist, currently working at Coimbra University; companion and moral support to one of the authors (CMS).

Comparative Remarks: *Scaphella carlae* new species differs from the North Sea Basin Pliocene species *S. lamberti* in having a more elongate shell, with a higher spire, the spire whorls are relatively taller and the last whorl less inflated, the outer lip is convex in profile and not sinuous as in *S. lamberti*, and the aperture is relatively smaller and much narrower. The protoconch of *S. carlae* consists of 1.5 flattened whorls, with a small blunt calcarella at the apex. The protoconch of *S. lamberti* comprises about two whorls, is smaller (7.3 versus 9.3 mm diameter), rounded, and more bulbous. Marquet (1997) discussed the variability in height/width ratio of *S. lamberti* in his Belgian assemblage. His ratio was 2.1 to 2.7 (average: 2.4). This is identical to the variability we have found (Figure 58) for the specimens of *S. lamberti* examined (BLP coll.), 2.1 to 2.6 (average: 2.3). These contrast markedly with the range observed in *S. carlae*, 2.7 to 3.1 (average: 2.9).

High-spired and elongate *Scaphella bolli* from the middle Miocene North Sea Basin is more similar in shape to *S. carlae* than *S. lamberti*. Indeed, the range of height/width observed by Marquet (1997), 2.8 to 3.1 (average: 2.96) is about the same as that for *S. carlae*. However, *S. bolli* has fewer columellar folds (3–4 versus 4–5), the spiral sculpture is more strongly developed and the protoconch is even smaller (5.3 mm diameter), with the first whorl even more bulbous and the calcarella more pointed in *S. bolli* than in *S. carlae*.

The middle Miocene Atlantic species *Scaphella miocaenica* (Figure 18) from the Loire Basin has a broader, squatter, more solid shell, with more shouldered whorls. The protoconch is rather similar in shape to that of *S. carlae*, with 1.5 flattened whorls and a small blunt calcarella at the apex, but much smaller (7.0 versus 9.3 mm diameter).

Scaphella tarbelliana (Grateloup, 1840) from the Atlantic lower and middle Miocene Aquitaine Basin (Figures 30–31) has characters intermediate between those of *S. carlae* and *S. lamberti*. The protoconch of *S. tarbelliana* is about 6.2 mm diameter. It is smaller, narrower and less inflated than *S. lamberti*, but still broader, with a proportionally lower spire than *S. carlae*. The outer lip is convex in profile and not sinuous as in *S. lamberti*, and

Figures 32–51. *Scaphella* species. **32–33.** *Scaphella* sp., juvenile (CMS coll.). Vale de Freixo, Pombal Region, central-western Portugal. Uppermost Zanclean to lowermost Piacenzian, lower-middle Pliocene, height 54.6 mm. **34.** *Scaphella* sp., juvenile (CMS coll.). Vale de Freixo, Pombal Region, central-western Portugal. Uppermost Zanclean to lowermost Piacenzian, lower-middle Pliocene, height 31.4 mm. **35–37.** *Scaphella miocaenica* (Fischer and Tournouër, 1879), juvenile (BLP coll.). Ferrière-Larçon, Loire Basin, France, Serravallian, middle Miocene, height 19.5 mm. **38–40.** *Scaphella* sp., juvenile (M/V coll.). Bonares, Guadalquivir Basin, Spain, Zanclean, lower Pliocene, height 34.1 mm. **41–43.** *Scaphella* sp., juvenile (M/V coll.). Bonares, Guadalquivir Basin, Spain, Zanclean, lower Pliocene, height 34.0 mm. **44–45.** *Scaphella lamberti* (Sowerby, 1816), juvenile (BLP coll.). Vrasenedok, Kallo, Oost-Vlaanderen, Antwerp, Belgium, Oorderen Sands, middle Pliocene, height 38.8 mm. **46–47.** *Scaphella lamberti* (Sowerby, 1816), juvenile (BLP coll.). Vrasenedok, Kallo, Oost-Vlaanderen, Antwerp, Belgium, Oorderen Sands, middle Pliocene, height 35.0 mm. **48.** *Scaphella lamberti* (Sowerby, 1816), juvenile (BLP coll.). Vrasenedok, Kallo, Oost-Vlaanderen, Antwerp, Belgium, Oorderen Sands, middle Pliocene, height 32.0 mm. **49–51.** *Scaphella carlae* new species juvenile (BLP coll.). Velerín Conglomerates, Velerín, Estepona. Spain, lower Piacenzian, middle Pliocene, height 47.5 mm.

the aperture intermediate in width between the two. Nevertheless, the overall outline of *S. tarbelliana* is still considerably more inflated than that of *S. carlae*. *Scaphella miocaenica* differs from *S. tarbelliana* in being thicker-shelled, squatter, and in having a lower spire and a more inflated, more shouldered last whorl.

Glibert (1952) noted that even at the juvenile stage *S. miocaenica* and *S. lamberti* were quite different, however, the character of the juvenile shell was not considered by subsequent authors. Certainly the juvenile shell of *S. miocaenica* is quite different from that of *S. lamberti* and *S. carlae*, being much broader, and the protoconch whorls more depressed. The shape of the juvenile shell of *S. carlae* is similar to *S. lamberti*, but in the latter the apex is more rounded, the calcarella more elevated and the diameter of the first teleoconch whorl is smaller.

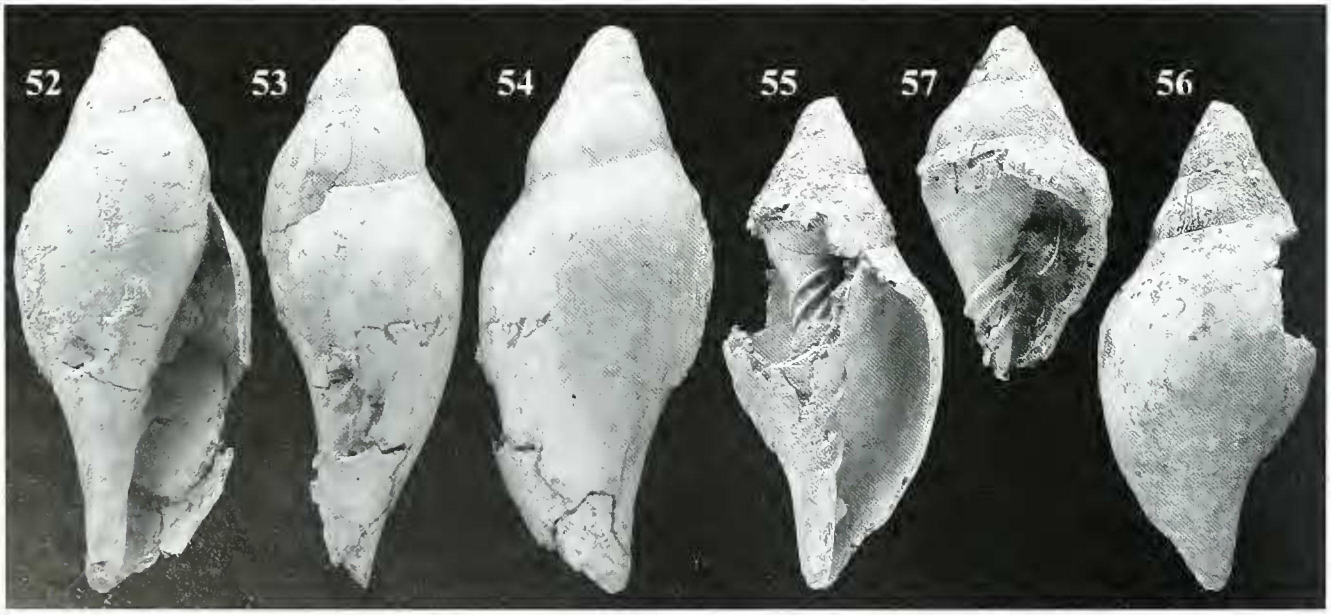
Scaphella sp.
(Figures 38–43, 52–57)

Description: Shell large, fusiform, relatively thick-shelled. Protoconch with about 1.5 smooth, flattened whorls, with small, blunt-pointed calcarella. Junction with teleoconch not sharply delimited. Teleoconch with 3–3.5 whorls. First teleoconch whorl short, flat, width about three times height. Second teleoconch whorl weakly angular in profile, increasing in height rapidly, so that suture becomes more oblique than on first whorl. Last whorl about 86% of total height, inflated, shouldered weakly a short distance below suture. Sculpture of very faint to obsolete spiral threads, most evident on early whorls and below suture. Aperture 74% of total height. Outer lip broken in examined specimen. Columella almost straight, bearing four narrow, elevated, oblique columellar folds, increasingly oblique abapically; adapical three folds of roughly equal strength, abapical fold much weaker. Columellar and parietal callus not preserved. Siphonal canal long and straight. Siphonal fasciole absent.

Dimensions and Material: Maximum height: 112.0 mm (although incomplete specimens suggest up to approximately 130 mm). Four specimens, BLP coll.; six specimens, M-V coll. All from Bonares, Guadalquivir Basin, Huelva, Spain. Zanclean, lower Pliocene.

Discussion: Despite intensive collecting by one of the authors (BL) and dedicated local collectors Manuel Molin and Daniela Velo for more than 30 years, only six incomplete adults and two juveniles have been found in the Guadalquivir Basin deposits. However, it is clearly not conspecific with *Scaphella carlae*. The lower Pliocene Atlantic specimens from the Guadalquivir Basin are thicker-shelled (maximum shell thickness 4.9 mm), squatter, with fewer whorls, the last whorl distinctly shouldered as opposed to convex or weakly shouldered, and there are only four columellar folds, which are narrower than in the coeval Mediterranean *S. carlae*. The maximum diameter of the protoconch (9.7 mm) is similar to that of *S. carlae*.

Of all the European species of *Scaphella*, the Guadalquivir Basin shells are most similar to the Atlantic middle Miocene Serravallian *S. miocaenica* from the Loire Basin of France. This latter species is also relatively squat, thick-shelled, with the last whorl shouldered, and with four folds on the columella. The protoconch diameter of *Scaphella* sp. is, however, greater than in *S. miocaenica* (9.7 versus 7.0 mm). The juvenile stage of *S. miocaenica* is quite characteristic, the last whorl very broad (Figures 35–37), unlike that of *S. lamberti* or *S.*



Figures 52–57. *Scaphella* sp. (BLP coll.), Bonares, Guadalquivir Basin, Spain, Zanclean, lower Pliocene. **52–54.** Height 98.7 mm. **55–56.** Height 112.2 mm. **57.** Height 90.4 mm.

carlae. Fortunately, two perfectly preserved juvenile specimens are available to us collected by Manuel Molin and Daniela Velo. The shape of the juvenile shell is most similar to that of *S. miocaenica*, possibly even more inflated, but larger at the same number of whorls, and the diameter of the protoconch and first teleoconch whorls is greater.

The specimens from the lower Pliocene Mondego Basin of Portugal (Silva, 2001) are both juvenile (Figures 32–34). Their protoconch characteristics and the shape of the juvenile shell are more similar to those of *Scaphella* sp. than *S. carlae*, and they have provisionally been added to the distribution.

CONCLUSIONS

In the Recent volutid faunas, non-planktotrophic larval development most likely induces the establishment of locally distinct populations, which ultimately results in poorly defined species-group taxa, as with the *Cymbiola* *pulchra* group from Queensland, Australia (Darragh and Ponder, 1998).

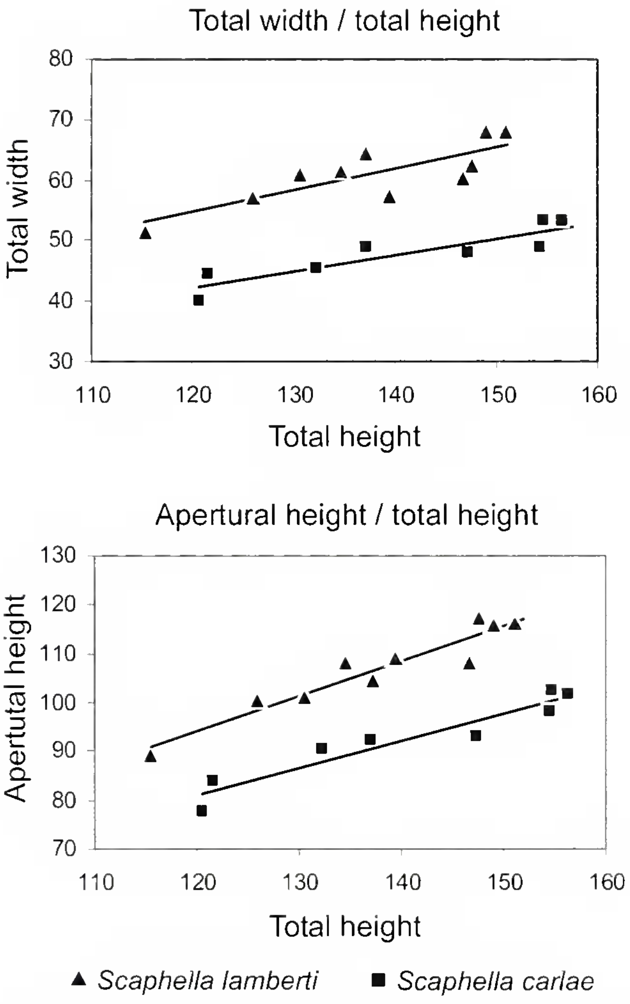


Figure 58. Morphometric comparisons between *Scaphella lamberti* and *S. carlae* new species. Measurements in mm.

The same applies to Recent *Scaphella* species in the New World, which explains the enormous discrepancy in the number of species recognized by different authors (four, Weaver and du Pont, 1970; 12, Clench, 1946). A similar situation occurs with European *Scaphella*, the species being restricted both geographically and stratigraphically. This is illustrated by the presence of two different species in the Atlantic Miocene Loire and Aquitaine Basins and the description of two coeval, but distinct species present on either side of the Straits of Gibraltar in the Pliocene. Most of the European species are relatively easily characterized, although the middle Miocene to lower Pliocene (lower to upper Redonian) *Scaphella* species from the Atlantic Loire Basin, northern France are less clearly distinguished. Brébion (1964) recorded the presence of both *S. miocaenica* and *S. lamberti* in these deposits and observed a transition from one to the other from the middle Miocene to the Pliocene.

This study of European *Scaphella* revealed that the genus as traditionally regarded is heterogeneous, with clear and consistent differences in shell morphology between Old and New World species. Old World *Scaphella* occur continuously in the European Cenozoic from the Paleocene to the middle Pliocene and form a distinct group from the Neogene to Recent New World species.

Assuming that Bondarev (1997) and Bandel (2003) are correct, and that that the Scaphellinae have a Cretaceous Tethyan origin, and that Dall (1907) is also correct, and that *Scaphella* originated from *Caricella*, it is hypothesized that the New World Paleocene *Scaphella* originated from a Cretaceous/Paleocene Old World ancestor, which emigrated to the New World from the Tethys, and that the Neogene New World *Scaphella* species are a distinct stock, which evolved from *Caricella*. This would explain the similarities between Old and New World Paleocene *Scaphella* and the differences with the New World Neogene stock. The European Paleocene to Pliocene species traditionally assigned to *Scaphella* therefore would constitute a separate stock from those in the New World, and might even correspond to a distinct genus-level taxon.

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